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Authors: Fowler, Denver W., and Sullivan, Robert M.

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The first giant titanosaurian sauropod from the Upper Cretaceous of North America

DENVER W. FOWLER and ROBERT M. SULLIVAN

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Argentinosaurus (Cenomanian, Argentina) is generally accepted as being the largest dinosaur so far discovered and is one of several giant titanosaurian sauropods known from the Upper Cretaceous of South America and Asia, but surprisingly not from North America. Here we present the first evidence of giant titanosaurian sauropods from the Upper Cretaceous of North America: two enormous vertebrae and a partial femur, from the Naashoibito Member of the Ojo Alamo Formation, New Mexico, and referred to *Alamosaurus sanjuanensis*. One of the new vertebrae, a posterior cervical, is comparable in size to a posterior cervical described for *Puertasaurus*: an *Argentinosaurus*-sized titanosaurian from the Maastrichtian of Argentina. This makes *A. sanjuanensis* the largest dinosaur from North America, and among the largest in the world. These findings indicate that *A. sanjuanensis* is diagnosed based on immature remains, which may have implications for cladistic analyses.

Key words: Dinosauria, Sauropoda, Titanosauria, *Alamosaurus*, body mass, Naashoibito Member, Ojo Alamo Formation, New Mexico, North America.

Denver W. Fowler [df9465@yahoo.co.uk], Museum of the Rockies & Department of Earth Sciences, Montana State University, 600 West Kagy Blvd, Bozeman, Montana;
Robert M. Sullivan [rsullivan@state.pa.us], The State Museum of Pennsylvania, 300 North St., Harrisburg, PA 17120.

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Introduction

Sauropod dinosaurs were the heaviest animals ever to have walked on land. They achieved gigantic body sizes relatively early in the reign of dinosaurs, dominating terrestrial herbivorous niches and reaching the acme of their diversity in the Late Jurassic (Upchurch and Barrett 2005). Despite this success, only two sauropod clades (Rebbachisauridae and Titanosauriformes; sensu Upchurch et al. 2004) survived through to the Cretaceous, and of these the Rebacchisauridae did not persist beyond the Cenomanian (Gallina and Apesteguia 2005), but one of these, the Titanosauria survived into the Late Cretaceous (Upchurch et al. 2004). By contrast, Cretaceous titanosauriforms flourished, enjoying a near-global distribution and attaining previously unrivalled body masses. The titanosaurian sauropod *Argentinosaurus* (Cenomanian, ~85 Ma, Argentina) weighed up to 73,000 kg (Mazzetta et al. 2004) and is generally accepted as being the largest dinosaur so far discovered (but see Carpenter 2006). *Argentinosaurus* is one of several giant titanosaurian sauropods known from the Upper Cretaceous of South America and Asia (Lü et al. 2009), but until now they have not been recognised from North America.

Fossils of modestly sized sauropod dinosaurs are commonly encountered in Lower Maastrichtian terrestrial deposits of the southwestern US. In 1922, Gilmore described the titanosaurian *Alamosaurus sanjuanensis* from a left scapula (USNM 10486, holotype) and right ischium (USNM 10487, paratype) collected from the Naashoibito Member of the Ojo Alamo Formation (Lower Maastrichtian, San Juan Basin, New Mexico). Subsequent finds were made in the Naashoibito Member (Lucas and Sullivan 2000; Jasinski et al. 2011) and other units across the southwest (McRae Formation, New Mexico, Wolberg et al. 1986; Javelina Formation, Texas, Lawson 1972; Lehman and Coulson 2002; North Horn Formation, Utah, Gilmore 1946) revealing that *Alamosaurus* was a medium-sized titanosaurian sauropod, weighing up to 32,663 kg (Lehman and Coulson 2002).

Recent finds by field crews from the State Museum of Pennsylvania force a reevaluation of the maximum body size of *A. sanjuanensis*. Here we describe two enormous vertebrae and a partial femur, collected from the Naashoibito Member of the Ojo Alamo Formation, New Mexico, and referred to *A. sanjuanensis*. These new specimens demonstrate that *A. sanjuanensis* grew much larger than previously suspected, rivalling the largest sauropods. Further, it is suggested that *A. sanjuanensis* is currently diagnosed based on immature material, which may have important implications for phylogenetic analysis.

Institutional abbreviations.—HM, Humboldt Museum, Berlin, Germany; MPM, Museo Padre Molina, Santa Cruz, Argentina; MUCPv, Museo de Geologia y Paleontologia de la Universidad Nacional del Comahue, Neuquén, Argentina;

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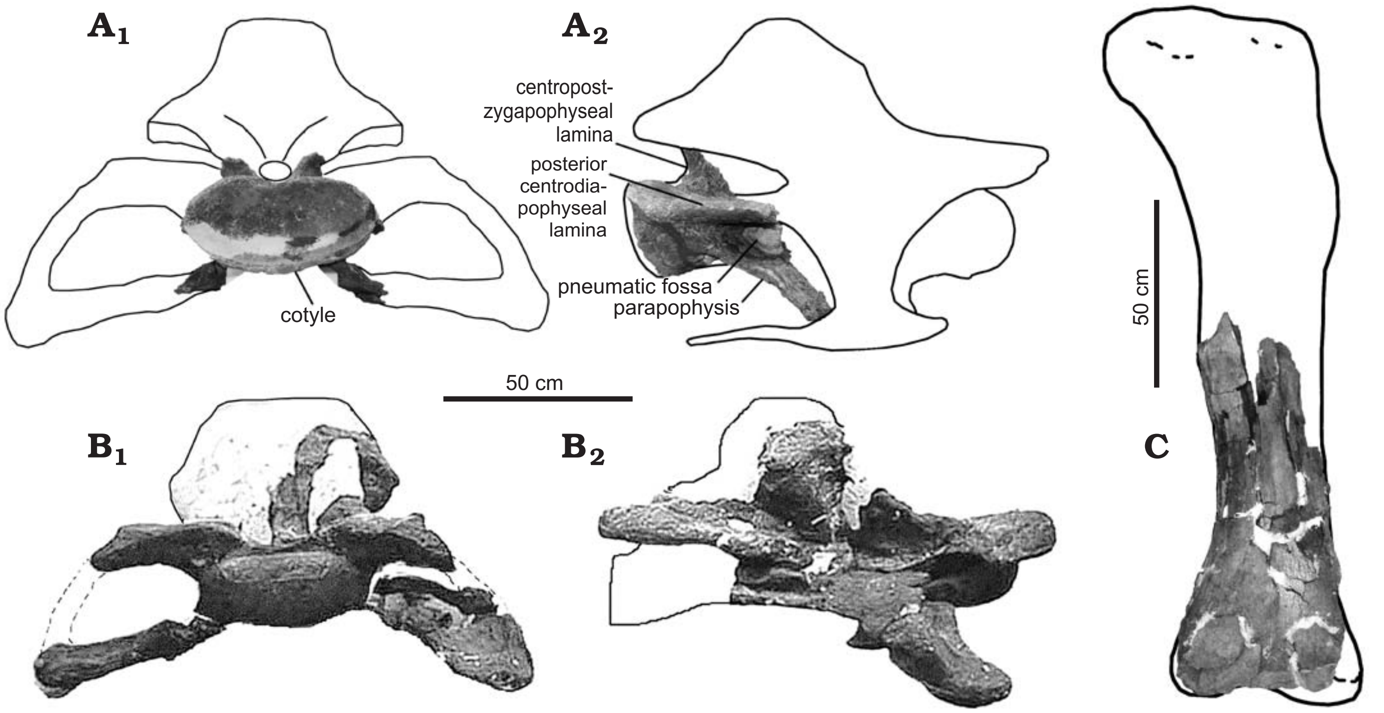

Fig. 1. Size comparison of *Alamosaurus sanjuanensis* (Gilmore, 1922) with *Puertasaurus reuili* Novas, Salgado, Calvo, and Agnolin, 2005 from the Lower Maastrichtian, Argentina. **A**. *Alamosaurus sanjuanensis* cervical vertebra, SMP VP-1850, in posterior (A_1) and right lateral (A_2) views. **B**. *Puertasaurus reuili* cervical vertebra, MPM 10002, in posterior (B_1) and right lateral (B_2) views (after Novas et al. 2005). **C**. *Alamosaurus sanjuanensis* distal end of left femur SMP VP-1625.

SMP, State Museum of Pennsylvania, Harrisburg, PA, USA; USNM, United States National Museum, Natural History Museum, Washington, D.C., USA.

Material

Distal portion of left femur (SMP VP-1625) collected in 2003 from De-na-zin Wash (SMP loc. 884b; Fig. 1C); SMP VP-1850, posterior cervical vertebra recovered in 2004 from Willow Wash (SMP loc. 389b; Fig. 1A); and SMP VP-2104, anterior caudal vertebra collected in 2006 from Willow Wash (SMP loc. 410b; Fig. 2B). See Table 1 for specimen measurements.

Table 1. Selected measurements (in cm) of newly described *Alamosaurus* material. Reconstructed measurement in parentheses.

Specimen	Measurement	
SMP VP-1850 (cervical vertebra)	preserved antero-posterior length	39 (112)
	preserved maximum centrum width	63 (70)
	preserved maximum width across parapophyses	71
	width of cotyle	50
	height of cotyle	26
SMP VP-2104 (caudal vertebra)	centrum length	13
	maximum preserved height	41.5 (70)
	maximum preserved width	35
	preserved condyle width	32.5
	preserved condyle height	26.5
	preserved cotyle width	31
	preserved cotyle height	22.7
SMP VP-1625 (femur)	preserved length	108.5 (185)
	preserved width across distal condyles	43

Geological setting

All specimens were collected from the Naashoibito Member (Lower Maastrichtian, Upper Cretaceous) of the Ojo Alamo Formation (San Juan Basin, New Mexico) but derive from different field localities, hence they are not associated and may come from different sized individuals. This is the type stratum and region of *Alamosaurus sanjuanensis*. Outcrop of the Naashoibito Member is geographically restricted to the southwestern portion of the San Juan Basin; from Hunter Wash in the northwest to Betonnie Tsosie Wash in the southeast (Baltz et al. 1966; Lucas and Sullivan 2000). The unit is very thin (maximum thickness 25.9 m, Barrel Springs, Dena-zin Wash; minimum 1.5 m, western branch of Ojo Alamo arroyo, Alamo Wash; Baltz et al. 1966) and as such is believed to represent a very short amount of geologic time (probably on the order of 500,000 years or less).

Description

The cervical vertebra SMP VP-1850 (Fig. 1A) has lost much of its anterior end and neural processes to recent erosion,

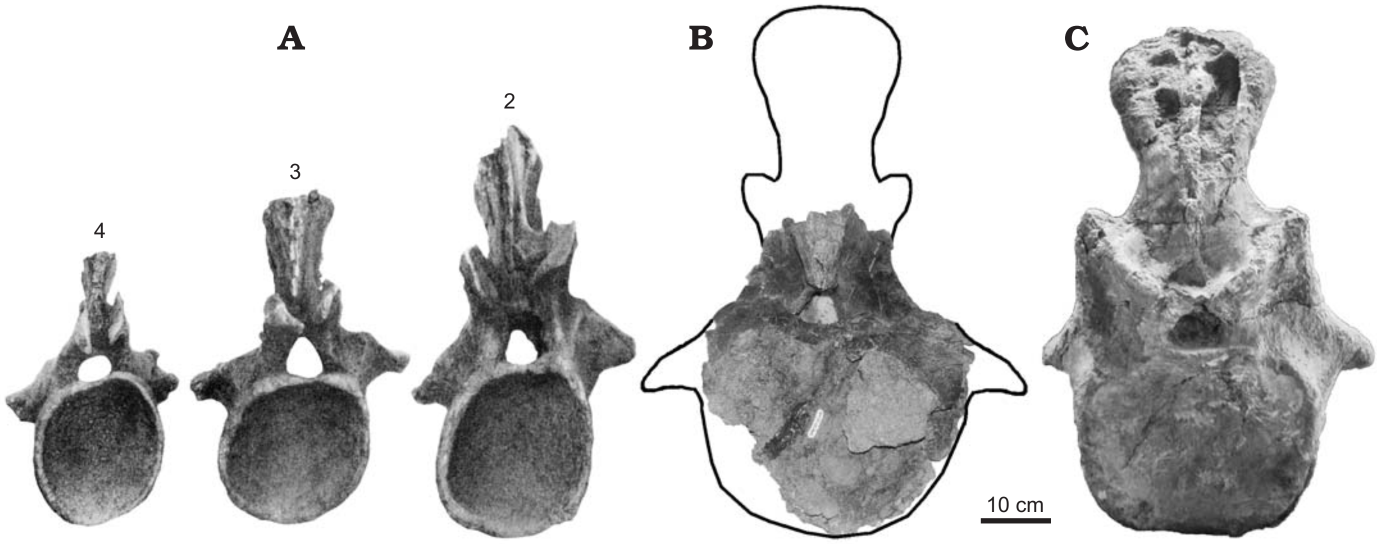

Fig. 2. Size comparison of *Alamosaurus sanjuanensis* (Gilmore, 1922) with *Futalognkosaurus dukei* Calvo, Porfiri, Gonzalez-Riga, and Kellner, 2007a from the Turonian, Argentina. **A**. *A. sanjuanensis* caudal vertebrae 2–4 from North Horn specimen (Gilmore 1946: pl. 8). **B**. *A. sanjuanensis* caudal vertebra (probably third or fourth) SMP VP-2104 in posterior view. **C**. *Futalognkosaurus dukei* caudal vertebra ?2, MUCPv-323, in anterior view (after Calvo et al. 2007b).

with only the posterior third of the centrum remaining. The cotyle is oval in shape and shows no sign of having been distorted by burial. Vertebral laminae are generally limited in extent and occurrence. The centropostzygapophyseal laminae (cpol) are mostly eroded away but what remain are broad, rather than thin or bladed. The posterior centrodiapophyseal lamina (pcdl) originates near the posterior border of the cotyle and forms a flat shelf, acting as the upper bound of the lateral pneumatic fossa (sensu Wedel 2003). The lateral pneumatic fossa is simple, undivided, and bowl-shaped, being gently depressed into the side of the centrum. The posterior ends of the parapophyses project 15 cm ventrally, but are damaged and incomplete. The internal structure is visible through the eroded sides of the centrum and is camellate, consisting of numerous small (<2 cm) irregularly branched camellae (similarly reported by Wedel 2003). The relatively short distance from the cotyle to the parapophyses of SMP VP-1850 suggest that it is a posterior cervical vertebra (also compared to the cervical series of *Giraffatitan* (*Brachiosaurus*) *brancai*; Janensch 1950). Lack of description of an entire or partial cervical series of *Alamosaurus sanjuanensis* or another giant titanosaurian prevents a more precise identification of its serial position.

The caudal vertebra SMP VP-2104 is quite strongly antero-posteriorly compressed, so much so that it is possibly a result of sediment compaction. The centrum is procoelous, with the anterior cotyle and posterior condyle reduced in prominence by the antero-posterior compression. The neural canal is roughly triangular. The neural spine is broken near the base, and the caudal ribs have been broken away. Although most of the vertebral laminae are not observable as a result of breakage, there does not seem to be any notable anterior or posterior centrodiapophyseal lamina, as the caudal rib grades gently into the side of the centrum.

The left femur SMP VP-1625 is ~30% complete, comprising most of the distal end. The condyles have been damaged by recent weathering, and much of the shaft is badly broken, such that a complete width measurement and cross sectional shape are unreliable to report. The fragmentary nature of SMP VP-1625 makes it only of use for size comparison.

Comparison

As only titanosaurian sauropods are known from the Late Cretaceous, it is most likely that the new remains pertain to this clade. Compared with those of other sauropod clades, titanosaurian cervical vertebrae are morphologically conservative, with reduced vertebral laminae (Wilson 2006). This is consistent with SMP VP-1850, supporting its assignment to the Titanosauria. The proportionally wide cotyle of SMP VP-1850 is only otherwise recorded in some titanosaurian cervical vertebrae (e.g., *Alamosaurus*, Lehman and Coulson 2002; *Malawisaurus*, Gomani 2005; *Puertasaurus*, Novas et al. 2005). Further morphological comparisons are hampered by the fragmentary nature of both other giant sauropods and the new specimens. The presence of lateral pneumatic fossae in SMP VP-1850 is unlike the giant Argentinean sauropods *Futalognkosaurus* (Turonian; Calvo et al. 2007b) and *Puertasaurus* (Early Maastrichtian; Fig. 1B; Novas et al. 2005), where such fossae are absent. In contrast, shallow to moderate lateral pneumatic fossae are present in cervical vertebrae of titanosaurians *Rapetosaurus* (Curry Rogers 2009), *Malawisaurus* (Gomani 2005), *Saltasaurus* (Powell 1992) and most importantly, *Alamosaurus* (Lehman and Coulson 2002).

Damage to SMP VP-2104 makes comparisons difficult. The single caudal vertebra known from *Futalognkosaurus*

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(Fig. 2C) is unlike SMP VP-2104 in being relatively broader across the neural arches, with caudal ribs positioned higher: at the level of the neural canal (although this may be mainly due to positional differences). Two mid-caudal centra are known from *Puertasaurus* (Novas et al. 2005) but these are not figured or described in detail, so comparisons cannot be made. In comparison to the caudal series of *Alamosaurus* (Fig. 2A; Gilmore 1946), the triangular neural canal of SMP VP-2104 is most similar to caudals 1–3, but the position of the caudal ribs below the neural canal is more similar to caudal vertebra 4 and later. We suspect that this represents individual or size-related variation. SMP VP-2104 cannot be caudal 1 because it is not biconvex, so probably corresponds to caudal 3 or 4.

Alamosaurus sanjuanensis is commonly assumed to be the only sauropod from the Maastrichtian of North America (Lucas and Sullivan 2000, and references therein). However, since the original description (Gilmore 1922), a considerable quantity of material from other titanosaurian taxa has been described, so much so that the type specimen of *A. sanjuanensis* (a scapula) was not considered diagnostic (Lucas and Sullivan 2000). Consequently, *A. sanjuanensis* was re-diagnosed based on the North Horn partial skeleton (Gilmore 1946) as lacking caudal ribs from caudal vertebra 9 and higher; having an acute rather than broad craniolateral process of the sternal plate (Upchurch et al. 2004); anterior and middle caudal vertebrae with several foramina opening at base of transverse process; posterior caudal vertebrae with notched ventral margins on anterior and posterior centrum faces; and ulnar shaft not stout (Wilson 2002). Thus, sauropod remains from the Late Cretaceous of North America are not immediately referable to *A. sanjuanensis* unless they happen to include caudal vertebrae, sterna, or ulnae. Unfortunately, caudal vertebra SMP VP-2104 is too damaged to assess whether or not it exhibits lateral foramina (Wilson 2002). However, all published diagnostic material displays these characters, so there is currently no evidence to suggest that more than one taxon of sauropod was present in the southern US during the Maastrichtian. Further, the argument that there may be more than one titanosaur taxon in the Naashoibito Member has not been formally proposed, nor is there any evidence to support this view. We therefore refer the new specimens to *A. sanjuanenis*, based on stratigraphic and geological parsimony, and the similarity of SMP VP-1850 to cervical vertebrae from Texas (Lehman and Coulson 2002), and SMP VP-1625 to the caudal series from Utah (Gilmore 1946).

The stratigraphy and age of *Alamosaurusus sanjuanensis*-bearing deposits has been a controversial subject (Sullivan and Lucas 2006; Lucas et al. 2009), but has important implications for the timing of land bridges with South America and Asia, associated faunal exchange, and the origin of *Alamosaurus*. Historically, *A. sanjuanensis* was considered as latest Maastrichtian in age and part of the assemblage of species present at the K-Pg boundary (Lawson 1972). However, strong doubt has been cast upon this view by recent stratigraphic work, including a radiometric date of 69 Ma from the Javelina Formation (Lehman et al. 2006), reassessment of the age of the North Horn Formation (Difley 2007), and new agreement over the likely age of the Naashoibito Member (Sullivan and Lucas 2006; Williamson and Weil 2008, 2009). Despite the debate over fine details, all workers accept a Maastrichtian age for *Alamosaurus*-bearing deposits.

Discussion

Although cervical vertebra SMP VP-1850 is incomplete, enough remains of the centrum for size assessment and comparison. The intact cotyle width of 50 cm is comparable to posterior cervical vertebrae known from other giant sauropods (largest available measurements given). The Late Jurassic basal titanosauriform *Giraffatitan* (*Brachiosaurus*) *brancai* is slightly smaller than SMP VP-1850, with cotylar widths of 47.2 cm and 46 cm for cervical vertebrae 12 and 13 respectively (HM SII, Janensch 1950). Cotylar heights of the Early Cretaceous titanosauriform *Sauroposeidon* are 20 cm and 27 cm for cervicals 6 and 8 respectively (although it might be expected that cervicals 12–13 of *Sauroposeidon* were larger; Wedel et al. 2000). Cotylar widths could not be measured directly, but CT scans suggest that the cotyle of C6 is taller than it is wide, making *Sauroposeidon* vertebrae smaller than SMP VP-1850. Explicit cotylar width measurements are not published for the derived Late Cretaceous titanosaurians *Puertasaurus* (Novas et al. 2005) and *Futalognkosaurus* (Calvo et al. 2007b) but published figures show that *Puertasaurus* (condylar width ~45 cm; Fig. 1B) is comparable in size to SMP VP-1850, with *Futalognkosaurus* slightly smaller (~40 cm).

The posterior centrum face width (32.5 cm) of anterior caudal vertebra SMP VP-2104 is much larger than any of the caudal series of *Alamosaurus* described by Gilmore (1946; centrum width of caudal 2, 19.5 cm; Fig. 2), and comparable in size to anterior caudal vertebrae of other giant sauropods (especially so considering that SMP VP-2104 probably corresponds to caudal vertebra 3 or 4, and centrum width decreases rapidly through *Alamosaurus* anterior caudal vertebrae). Caudals 1 and 2 of the giant titanosauriform *Paralititan* measure 29 and 27.5 cm respectively across the posterior centrum face (Lamanna 2004): slightly smaller than SMP VP-2104. Caudals 2 and 5 of *Giraffatitan* (*Brachiosaurus*) *brancai* measure 31.7 and 25 cm respectively across the posterior centrum face (HM SII; Janensch 1950). *Futalognkosaurus* preserves a single caudal vertebra which although identified as "probably the 1st" (Calvo et al. 2007) is procoelous, not biconvex, so probably corresponds to caudal 2 or later. It is stated as measuring 40 cm across the posterior face of the centrum (larger than SMP VP-2104), but appears substantially smaller (~31 cm) in the published figure.

Partial femur SMP VP-1625 is conservatively reconstructed as 185 cm in length, based on proportions of an *Alamosaurus* femur illustrated in Lehman and Coulson (2002). This is slightly smaller than other giant sauropods (*Giraffatitan*:

214 cm, Janensch 1961; *Brachiosaurus altithorax*: 203 cm, *Antarctosaurus giganteus*: 235 cm, *Antarctosaurus wichmannianus*: 186 cm, *Argentinosaurus* (reconstructed): 256 cm, Mazzetta et al. 2004). The femur may have come from an individual that was smaller than those represented by the vertebrae.

It is notoriously difficult to estimate body masses of extinct taxa, even for relatively complete skeletons (Sander et al. 2011). *Argentinosaurus* is considered to be the largest sauropod yet discovered, and is estimated to have weighed ~73,000 kg (Mazzetta et al. 2004), but is known from very little material. By comparison, Mazzetta et al. (2004) calculated the mass of *Giraffatitan* (*Brachiosaurus*) *brancai* as 39,500 kg, close to the estimate by Gunga et al. (2008) of 38,000 kg, established using different methods. Although 73,000 kg may seem extraordinarily large, *Argentinosaurus* and other derived giant titanosaurians had wide-gauge bodies and were probably considerably stockier than more basal titanosauriforms like *Giraffatitan*, although confirmation of this awaits discovery of more complete specimens.

It is not possible to reconstruct the maximum mass for *Alamosaurus* based on our new specimens, but it is clear that they are substantially larger than previous material, so some reassessment is appropriate. The body mass of *A. sanjuanensis* was previously estimated as 32,663 kg (Lehman and Coulson 2002), but this was calculated based on partial skeletons of considerably smaller individuals than represented by the material described here. Some indication that *A. sanjuanensis* grew to a larger adult body size was provided by histological analysis of a large femur from Texas which showed that an individual previously presumed to be mature was still growing (Woodward and Lehman 2009). SMP VP-1850 is similar, if not slightly larger than the cervical vertebrae of *Puertasaurus* and *Futalognkosaurus*, but mass estimates have not been published for these taxa. However, it has been suggested that *Puertasaurus* was of similar size to *Argentinosaurus* (Novas et al. 2005). Both *Puertasaurus* and *Argentinosaurus* are very incompletely known, with little overlapping material. However, Novas et al. (2005) stated that dorsal vertebra 2 of *Puertasaurus* is much wider across the transverse processes (168 cm) than dorsal ?4 of *Argentinosaurus* (although, dorsal vertebra ?2 of *Argentinosaurus* is 115 cm in height compared to 106 cm for *Puertasaurus*; Bonaparte and Coria 1993) . Thus, although tentative, *Puertasaurus* (and therefore *Alamosaurus*) would appear to be of comparable size to *Argentinosaurus*. This makes *A. sanjuanensis* the largest dinosaur from North America, and among the largest in the world. Moreover, since the remains of other taxa are so fragmentary, *A. sanjuanensis* is among the most completely known of all the giant titanosaurians, its remains comprising at least three partial skeletons and many isolated elements, representing an ontogenetic spectrum from juvenile (Lehman and Coulson 2002) to adult.

It is becoming increasingly clear that most dinosaurs appear to have perished before reaching adulthood (Varricchio 2011), so the probability of finding specimens of the largest individuals of any species is relatively low. The results of our analysis suggest that *Alamosaurus sanjuanensis* is diagnosed based on immature remains (Gilmore 1946; Upchurch et al. 2004; Wilson 2002). It has been recognized for some time that immature dinosaurs typically exhibit features more similar to their ancestors than to adults of their own species (Rozhdestvensky 1965). This may strongly affect the validity of characters that define taxa based on immature remains, and their consequent phylogenetic position. Despite significant morphological changes through ontogeny in sauropods (Wedel 2003; Whitlock et al. 2010; Woodruff and Fowler 2010), development remains poorly understood, even for well known taxa (Schwarz et al. 2007; Carballido et al. 2010). The abundance of *A. sanjuanensis* remains in Maastrichtian rocks of the southwestern United States offers the best opportunity to collect a statistically significant sample of any giant sauropod. Large sample population studies, such as histological analyses, are essential in elucidating the dinosaur growth trajectories that facilitated the evolution of gigantism.

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